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Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population

R. Kent Smedbol[1] and J.S. Wroblewski[2]

[1]Department of Oceanography
Dalhousie University
Halifax, NS B3H 1J5 Canada

and

[2]Fisheries Oceanography Group
Ocean Sciences Centre
Memorial University of Newfoundland
St. John's, NF A1B 3X9 Canada

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Abstract

Atlantic cod (*Gadus morhua*) population inhabiting the coastal and offshore regions of eastern Newfoundland and Labrador. Evidence for subpopulation structure is drawn from studies of spawning time and locations, morphometrics, and genetic differentiation. We identify putative subpopulations associated with spawning areas near offshore banks and in coastal bays. The historical northern cod population is first represented as an unfished metapopulation. We then modify the model to include the influence of fishing harvest on subpopulation extinction. Metapopulation theory predicts that fewer spawning areas are occupied as the population declines. This prediction is validated in that Saglek, Nain, Makkovik and Harrison Banks have had no significant spawning activity since the over exploitation by trawlers during the 1960s. The corollary prediction is that as the population recovers, currently unoccupied spawning areas will be recolonized. The model suggests a continued moratorium on fishing the remaining subpopulations would promote recolonization and accelerate the recovery of the overall metapopulation.

Résumé

On retrouve une population de morue de l'Atlantique (*Gadus morhua*) dans les régions côtière et hauturière de l'est de Terre-Neuve et du Labrador. Des études portant sur le moment et le lieu du frai, la morphométrie et la différenciation génétique montrent l'existence de sous-populations. Nous avons défini des sous-populations présumées correspondant à des zones de frai situées à proximité de bancs hauturiers et dans des baies côtières. Nous avons tout d'abord représenté la population historique de morue du Nord par une métapopulation non exploitée. Nous avons ensuite modifié le modèle afin de tenir compte de l'influence de la récolte par pêche sur l'extinction de sous-populations. La théorie de la métapopulation, prévoit que moins de lieux de frai sont occupés à mesure que la population s'appauvrit. Cette prévision est validée par le fait qu'il n'y a pratiquement aucune activité de frai appréciable aux bancs Saglek, Nain, Makkovik et Harrison depuis la surexploitation par chalutiers des années 1960. Cela a pour corollaire que les zones de frai actuellement désertées seront occupées de nouveau à mesure du rétablissement de la population. Le modèle indique que le maintien du moratoire de la pêche des sous-populations restantes devrait favoriser la recolonisation et accélérer le rétablissement de la métapopulation générale.

Introduction

Metapopulation theory (Hanskii & Gilpin 1997) has been used to describe the population structure of many terrestrial and freshwater species. Some examples include shrews (Peltonen & Hanskii 1991), butterflies (Hanskii 1994a), malleefowl (Day & Possingham 1995), and river fishes (Gotelli & Kelley 1993). These examples from diverse taxa hold in common the occupation of ranges comprised of heterogenous habitat.

Recently, marine scientists have identified metapopulation structure in marine fish populations. Man et al. (1995) considered metapopulation dynamics in modeling recruitment of reef fishes. McQuinn (1997) described the benthic spawning distribution of the Atlantic herring (*Clupea harengus*) within the metapopulation concept. Bailey (1998) and Bailey et al. (1999) have proposed the existence of metapopulation structure in the distribution of the semi-pelagic walleye pollock (*Theragra chalcogramma*) of the North Pacific.

We contend that the northern Atlantic cod (*Gadus morhua*), a demersal fish species with a large geographic range off eastern Newfoundland and Labrador (Fig. 1), is distributed as a metapopulation during the spawning season. Adult fish exhibit interannual fidelity to geographical spawning areas.

The metapopulation

A metapopulation is a set of local populations or subpopulations within some larger area (usually the population's range) where movement from one subpopulation to another subpopulation is possible (Hanskii & Simberloff 1997). Metapopulation theory describes the spatial dynamics of interconnected subpopulations (Fig. 2). The degree of segregation between subpopulations may range from slight to almost complete isolation, depending upon factors such as the distance between areas occupied, geographic (or oceanographic) barriers between areas, and the dispersive ability of the species (Harrison & Taylor 1997). Exchange between the subpopulations of the metapopulation prevents the development of separate, autonomous populations. As a result, metapopulation subpopulations may not (and need not) be genetically distinct, although such differentiation is suggestive of the existence of metapopulation structure with low levels of exchange between subpopulations.

In the simplest metapopulation model first proposed by Levins (1970), there are three assumptions: subpopulations have the same geographic extent and degree of isolation, each subpopulation has separate local population dynamics, and the rate of exchange of individuals among subpopulations is too low to affect local population dynamics. Hanskii & Simberloff (1997) suggest that of main importance is the idea of discrete local breeding populations connected by immigration and emigration.

In the Levins model, areas which can support subpopulations are considered either occupied or unoccupied. The abundance of a local subpopulation is assumed to be either nil (empty area) or at the carrying capacity of the environment (fully occupied area).

Although abundance is not explicitly included in the model, investigations by Hanskii (1991) have shown that colonization is proportional to overall metapopulation abundance, due to a "rescue effect" at high abundance in which immigrants from other subpopulations enhance subpopulation persistence. Extinction is considered to be equally likely for all subpopulations (a constant).

The northern Atlantic cod population

The Labrador-East Newfoundland stock complex of Atlantic cod (*Gadus morhua*) has a geographic range exceeding 15 degrees of latitude, extending from northern Labrador to the northern Grand Bank (Fig. 1) (Templeman 1979, Lear & Parsons 1993). For management purposes this stock complex was divided into two sections when the northern region failed to recover following the collapse in abundance in the late 1960s due to over exploitation (Pinhorn 1976). These two sections are the Northern Labrador Portion located in NAFO Divisions 2G and 2H, and the Southern Labrador-East Newfoundland Portion (the "northern cod stock") of NAFO Divisions 2J3KL (Lear & Parsons 1993).

The northern cod population, however, should by definition include all fish that live within the overall range of the Labrador-East Newfoundland stock complex as identified by Templeman (1979). For the purposes of this paper, we consider the northern cod population to consist of those cod that occupy the range from Cape Chidley, at the northern tip of Labrador, to the northern portion of the Grand Bank, and encompassing all of the coastal, shelf, and shelf-edge regions in between (Fig. 1). Hereinafter, the term "northern cod population" will refer to the Atlantic cod population in 2G, 2H, 2J, 3K, and 3L.

Historically, Atlantic cod, which inhabited the shelf regions off Labrador and eastern Newfoundland, exhibited annual spawning and feeding migrations (Lear 1984, Lear & Green 1984). Spawning began in late winter and continued for up to four months, with spawning occurring earlier in the north and progressively later to the south (Myers et al. 1993). Spawning occurred primarily over the offshore banks and along the shelf edge (Templeman 1979, Taggart et al. 1994, Wroblewski et al. 1995), with some spawning occurring across the entire shelf (Hutchings et al. 1993) and in the bays of northeast Newfoundland (Hutchings et al. 1993, Brattey 1997, Smedbol & Wroblewski 1997, Smedbol et al. 1998). Following spawning offshore on the continental shelf, many adults migrated inshore to feed during the summer, and returned offshore in the late autumn and early winter (Lear 1984, Lear & Green 1984, Rose 1993). Some adults remained on the shelf year-round (Taggart 1997).

Early studies indicated that the Labrador-East Newfoundland stock complex was not a panmictic unit, but rather contained a number of partially isolated subcomponents. Based on mark-recapture studies, Templeman (1962, 1979) postulated that the stock complex contained many local populations. Lear (1984) presented evidence for homing to specific offshore overwintering and spawning areas, with some straying. These tagging studies also provide evidence for year-round residency of particular offshore regions. Lear (1984) reported that a component of the cod assemblage found on the northern Grand Bank does

not migrate inshore following spawning, but rather resides on the Bank during the summer months. Mark-recapture data also suggest residency within the coastal bays (Taggart et al. 1995, Wroblewski et al. 1996). Some adult fish occupy inshore regions throughout the year (Goddard et al. 1994, Wroblewski et al. 1994).

Recently, analyses of microsatellite DNA allele frequency variation at the population level have provided evidence for subpopulation structure. Bentzen et al. (1996) detected genetic differences between samples of cod from the Hamilton-Belle Isle-Funk Island Bank region and samples from the Northern Grand Bank area (Fig 1). That study was extended to include samples from inshore areas (Ruzzante et al. 1996, Ruzzante et al. 1997, Ruzzante et al. 1998, Ruzzante et al. 2000), resulting in the detection of four possible subpopulations of the northern cod population, associated with Hamilton-Belle Isle-Funk Island Bank, the Northern Grand Bank, Trinity Bay and Gilbert Bay (Fig. 1). A study using different microsatellite loci (T. Beacham, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC, personal communication) also suggests the existence of subpopulation structure.

The northern cod population as a metapopulation

We contend that during the spawning period the northern cod population resembles a metapopulation. The geographic location of subpopulations is associated with overwintering/spawning areas. Some local populations have distinguishing characteristics: genetic distinctiveness (microsatellite DNA allele frequency variation), phenetic distinctiveness (length-at-age, weight-at-age, fecundity-at-age), and residency in or interannual fidelity to discrete spawning areas (Ruzzante et al. 2000). The physical oceanographic processes and fish behaviours that result in the semi-isolation of these subpopulations are poorly understood. However, the evidence points to the existence of such structure.

The genetic data (e.g. Ruzzante et al. 1997, Ruzzante et al. 2000) suggest that some subpopulations are more isolated reproductively than others. This departs from the simplest metapopulation model (Fig. 2a) of Levins (1970), but metapopulations that conform to the assumptions of Levins (1970) may be rare (Harrison & Taylor 1997). The northern cod population may conform to the "mixed structure" metapopulation model of Harrison & Taylor (1997), wherein the metapopulation includes local populations with high rates of exchange functioning as a single subpopulation, and more isolated subpopulations (Fig. 2b).

Genetic differentiation among subpopulations can arise through a number of processes, including natural selection, mutation, genetic drift, and the restriction of gene flow among subpopulations. The studies cited above used microsattelite DNA, which is assumed to be non-coding, neutral DNA (e.g. Park & Moran 1994). As such, it is unlikely that the genetic structure reported in those studies was a result of selection. For genetic differentiation to develop among subpopulations in the absence of selection and outbreeding depression, some local process of larval retention or natal philopatry is necessary. Figure 3 depicts

mechanisms that may result in this semi-isolation of subpopulations. Wind events and eddy currents affect egg and larval drift (Helbig et al. 1992, Davidson & deYoung 1995). Larvae that settle away from nursery grounds may be lost to the subpopulation (e.g. Sinclair 1988), but may function in colonization. As juveniles mature, they join the adult migration to the spawning area (Harden-Jones 1968, Lear & Green 1984). Inshore, juveniles may mature within their natal bays.

Subpopulations of the northern cod metapopulation

Evidence for localized spawning, some of which are no longer occupied, is derived from a variety of data sources.

Saglek, Nain, Makkovik and Harrison Banks

The most northerly region identified as a major spawning location is the shelf break area of Saglek Bank in NAFO Division 2G (Fig. 1). Postolaky (1965) sampled prespawning and spawning aggregations of cod in this area during the spring (March-April), at depths of 280-350 m. Newly spawned eggs were also found in this area during April (Postolaky 1965). The Saglek Bank area produced the highest number of recently spawned eggs during his study. The next major spawning location was determined to lie along the shelf break of Nain Bank in NAFO Division 2H (Fig. 1). Postolaky (1965) captured spawning cod and sampled cod eggs in this area during April. The area of Makkovik and Harrison Banks near the Division 2H-2J border (Fig. 1) is included in the metapopulation model because of the discovery of early stage cod eggs in this region by Serebryakov (1967), again in the early spring. Significant spawning no longer occurs on or near these banks (DFO 1999).

Hamilton, Belle Isle-Funk Island Banks

Until the early 1990s the eastern slopes of Hamilton Bank and Belle Isle-Funk Island Bank (Fig. 1) was a major spawning area. Cod eggs were sampled in the region by Serebryakov (1967) and the presence of spawning aggregations was reported by Templeman & May (1965). Hutchings (1996) reported interannually consistent, high density catches of cod in research trawl surveys of these banks during the late fall from 1981-1992. Using data from commercial trawlers, Wroblewski et al. (1995) concluded that cod spawned along the shelf edge in this region. Rose (1993) and Rose et al. (1995) observed cod spawning on the continental shelf near the boundary of NAFO Divisions 3K and 3L (Fig. 1), at the eastern terminus of the inshore migration path known as the Bonavista Corridor. Cod occupying the Hamilton, Belle Isle-Funk Isle, Bonavista Corridor spawning regions may have functioned as a "mixed subpopulation" (Fig. 2b). Very few mature cod are presently found at these offshore locations (DFO 1999).

Northern Grand Bank

The most southerly spawning region is located on the northern section of the Grand Banks in Division 3L (Fig. 1). Evidence for cod spawning in this area is present in research trawl surveys (Hutchings et al. 1993), tagging studies (Templeman 1962, Templeman and Fleming 1962), and commercial catches (Kulka et al. 1995, Wroblewski et al. 1995).

Labrador Bays

Northern Atlantic cod, which are genetically distinct from all other known subpopulations, inhabit Gilbert Bay, southern Labrador (Ruzzante et al. 2000). While cod in spawning condition have been sampled in Gilbert Bay, few data exist on cod spawning along the Labrador coast (Fig. 1). There are historical reports of northern cod inhabiting Groswater Bay and Sandwich Bay, Labrador (Fig. 1) (H. Best, Labrador Institute, Memorial University of Newfoundland, St. John's, personal communication). These locations are noted in Fig. 1, but are not given the status of subpopulation due to the lack of data on spawning.

Northeast Newfoundland Bays

Evidence for cod spawning in the bays of eastern Newfoundland is present in egg and larval surveys (Smedbol & Wroblewski 1997, Smedbol et al. 1998) and the observed age distribution of pelagic (Anderson & Dalley 1997) and post-settlement (Methven & Badjic 1994, Pinsent & Methven 1997) juvenile cod. Research trawl and gillnet surveys found cod in spawning condition in Bonavista Bay and Trinity Bay (Hutchings et al. 1993). Spawning aggregations of cod were observed in Trinity Bay by Brattey (1997) and by Smedbol & Wroblewski (1997). Fishers' ecological knowledge of "bay cod" in Bonavista and Trinity Bay has been documented by Neis et al. (1999). As tagging studies found movement of cod between Trinity Bay and bays to the north (Brattey 1997), cod resident in coastal waters of eastern Newfoundland are considered members of a single "mixed subpopulation" (Fig. 1).

Northern cod metapopulation dynamics

At high population abundance, metapopulation theory predicts that most suitable habitats will be occupied (e.g. Hanski 1991). In the metapopulation model for northern cod, this means the occupancy of most, if not all, of the major spawning areas. We contend that during the historical period of high abundance prior to over exploitation during the 1960s (Bishop et al. 1993), all these proposed subpopulations of the northern cod population existed. Several authors have noted this spatial "stability" in spawning locations, as evident in mark-recapture studies (Templeman 1979, Lear 1984, Taggart et al. 1994).

When the northern cod population collapsed totally in the early 1990s (Hutchings & Myers 1994), the range of the population apparently had not simply contracted. Rather, fish were found at fewer overwintering/spawning areas (Kulka et al. 1995, Hutchings 1996, Rice 1997). The change in distribution has been interpreted as a southerly shift due to

environmental changes (deYoung & Rose 1993), and (or) prey distribution (Rose et al. 1994). Alternatively, overfishing may have forced some subpopulations to commercial extinction (Larkin 1977, Myers et al. 1997a). The current spatial structure of the population during the overwintering/spawning season appears to be discrete, with aggregations of overwintering/spawning adults occupying only a few areas such as Smith Sound, Trinity Bay (Smedbol et al. 1998) and Tobins Point (49° 30' N, 50o 30' W) on the northern Grand Bank (Rose 1996). Very few adult cod are dispersed across the continental shelf (Hutchings 1996, Shelton et al. 1996, Rice 1997).

In the following modeling exercise, we first develop a basic metapopulation model for the historical northern cod population. We then consider the effects of commercial harvest on the metapopulation dynamics. We model the extirpation of subpopulations during the population decline. Finally, we develop predictions for recolonization of currently unoccupied spawning areas during a future population recovery.

The model

A model for northern cod population structure is derived from the basic metapopulation equation as presented by Levins (1970). The Levins (1970) model, in its simplest form, can be expressed as:

$$\frac{dP}{dt} = mP(1-p) - eP \qquad (1)$$

where P is the fraction of subpopulation areas occupied at time t, m is the "colonization" parameter, and e is the "extinction" parameter. The rate of colonization of empty habitats is assumed to be proportional to $P(1 - P)$, where $P < 1$.

The equilibrium value of P is:

$$P_E = 1 - \frac{e}{m} \qquad (2)$$

and therefore the metapopulation will persist as long as $e/m < 1$. For persistence to occur, recolonization must occur at a sufficiently high rate within the metapopulation to offset the rate of extinctions (Hanskii 1997).

In our model for northern Atlantic cod, P represents the proportion of major spawning areas that are occupied, analogous to the proportion of occupied habitat patches in models for terrestrial species (Hanskii 1994a). In terms of our hypothesis, an important assumption is that an individual breeds in only one area during a single spawning season. The particular spawning area in which an adult spawns may differ between years (exchange between subpopulations), but the individual must spawn in only one area per year for metapopulation theory to apply.

Parameter estimates for the simple model may be derived from an analysis of cod life history on appropriate time scales. Metapopulation dynamics concern the turnover of subpopulations rather than individuals. We estimate colonization and extinction rates for northern cod subcomponent areas as follows.

The extinction parameter

Gadus morhua can survive to a considerable age, with one northern Atlantic cod as old as 29 years recorded (Scott & Scott 1988). However, cod very rarely exceed 25 years of age (Shelton et al. 1996). We use the maximum lifespan to arrive at rates of extinction ($-eP$) in our model. A subpopulation will not become "extinct" (the spawning area unoccupied) unless reproduction has been unsuccessful for the entire lifetime of the youngest individuals in the subpopulation. In addition, there must be no substantial immigration into the subpopulation (no rescue effect). The period from birth to death of the youngest individuals can be no longer than the maximum lifespan of 29 years. Therefore, the extinction parameter is of the order 1 per 29 years, or $e = 0.03\ yr^{-1}$. The conditions of little or no substantial immigration and successive years of reproductive failure were not likely experienced by historic subpopulations, given the abundance and age structure of this population (> 109 adults aged 6+ years in the early 1960s, Taggart et al. 1994).

The recolonization parameter

The mechanism by which empty spawning areas are recolonized is not resolved in this simple model. However, we envision that the agents of recolonization of unoccupied areas are groups of adult cod, settling pelagic juveniles, or both (Fig. 3). Recolonization of northern areas would likely be accomplished by adult fish swimming against the mean flow (Labrador Current). Areas downstream may be recolonized by either adult fish, or settling juveniles (deYoung and Rose 1993). Shoals of adult fish often travel long distances (Rose et al. 1995, Wroblewski et al. 1995) and may end up spawning in new areas. An example of such relocation may be the aggregation of cod detected in Smith Sound, Trinity Bay in April 1995 (Rose 1996, Ruzzante et al. 1997, Smedbol et al. 1998).

With the paucity of data on recolonization of subpopulations of northern cod, we estimate the recolonization parameter indirectly. We examine literature sources to estimate historic values of P_E, and use Eq. (2) to derive a value for m knowing P_E and e. During the late 1800s and early 1900s, a commercial fishery was prosecuted across the entire latitudinal range of the population, from the northern area of the Grand Bank to Cape Chidley at the northern tip of Labrador (Lear & Parsons 1993). This indicates that most areas were occupied. However, during its history the northern cod fishery exhibited substantial variation in total catch and in catch per unit effort at regional (i.e. subpopulation) spatial scales (Lear & Parsons 1993, Figs. 2 and 3, Hutchings & Myers 1995, Fig. 2). Fisheries for Icelandic and Norwegian cod show analogous variation, to the point of local fishery collapse (e.g. Jónsson 1994, Øiestad 1994). We conclude that prior to the over-exploitation

by otter trawlers during the 1960s, at least 90% of the major spawning areas of the northern cod population depicted in Fig. 1 were occupied ($P_E = 0.9$). We then solve for the value of m using values of $P_E = 0.9$ and $e = 0.03$ yr^{-1} under equilibrium conditions (Eq. 2). Therefore, $m = 0.3$ yr^{-1}.

The effect of fishing

The northern cod population has been harvested (subsistence and commercial fishing), for approximately 500 years (Hutchings & Myers 1995). The potential contribution of fishing mortality to the extinction of subpopulations of northern cod cannot be ignored. We incorporate the impact of fishing on the metapopulation dynamics by adding to the extinction parameter e a component representing harvest, such that $e = e_N + e_F$, where e_N is the natural extinction process, and e_F is the influence of fishing. Our extended Levins model for northern cod then becomes:

$$\frac{dP}{dt} = mP(1-p) - (e_N - e_F)P \qquad (3)$$

If e_F is negligible, P_E remains approximately 0.9. Considering long-term records of the fishery, the northern cod population has only recently (since the 1960s) undergone an overall decline. The historical effect of fishing on metapopulation dynamics must have been relatively small ($e_F < e_N$).

Sensitivity analysis

An analytical sensitivity analysis determines the relative response of the model to its parameter values. Equations that describe the change in the fraction of subpopulation areas occupied (P) with respect to changes in the recolonization (m) and extinction (e) parameters are:

$$\frac{\partial P}{\partial m} = \frac{1-P}{m} \qquad (4)$$

and

$$\frac{\partial P}{\partial e} = \frac{-1}{m} \qquad (5)$$

The time dependent solutions of Eq. (3) were computed to investigate the behaviour of the model with different initial values of P. This procedure also permitted the analysis of the effect of over exploitation on the rate of extinction of subpopulations.

Model results

Equilibrium solutions of the Levins model (Eq. 1) for various values of the colonization (m) and extinction (e) parameters are presented in Figs. 4 and 5. The proportion of subpopulation areas occupied increases from zero as the colonization parameter exceeds the extinction parameter. If m is twice the value of e, then half of the suitable areas will be occupied, and 90 % of the areas are utilized if m is 10 times larger than e.

Metapopulation temporal dynamics

Several generalizations can be made by examining the time-dependent solutions presented in Fig. 6. First, the time to reach equilibrium increases as the initial P value departs further from P_E (Fig. 6a, Table 1). Second, as the colonization parameter (m) is reduced, the time to reach equilibrium increases for all initial values of P, and P_E is lowered, i.e. the proportion of occupied subpopulation areas at equilibrium is reduced (compare Figs. 6a and 6b). The effect of doubling the extinction parameter (e) is comparable, but not identical, to the effect of halving the colonization parameter (m) (compare Figs. 6a, 6b and 6c). The time required to reach equilibrium does not lengthen as quickly as under a regimen of decreasing colonization rate. However, in both cases there is a change in equilibrium occupancy from $P_E = 0.9$ to 0.8.

A metapopulation collapse

Fig. 6d presents the condition of near total "metapopulation collapse". An eightfold increase in the value of the extinction parameter ($e = 0.24$) changes the equilibrium occupancy (P_E) from 0.9 to 0.2. The decline from initial values of P and the approach to the new equilibrium value occurs relatively quickly. Most of the decline occurs during the first 10 years of the model run, and the model has nearly attained equilibrium occupancy by 20 years (Fig. 6d).

Analytical Sensitivity analysis

Eq (4) states that the change in occupancy due to a change in the colonization parameter is dependent upon (1 - P), whereas Eq (5) states that the change in P due to a change in the extinction parameter is independent of P. As a result, when P is close to unity, the model is more sensitive to changes in e. When P is small, changes in m are more influential. For instance, doubling m from 0.3 to 0.6 yr^{-1} results an increase of P from 0.9 to 0.95 at equilibrium, an increase of 5.3 %. Increasing e from 0.03 to 0.06 yr^{-1} causes a drop in the equilibrium P from 0.9 to 0.8, a decrease of 11 %, or near twice the change caused by an equivalent doubling of m. When P is small (0.2), doubling m (0.3 to 0.6 yr^{-1}) causes a 300 % increase in P (0.2 to 0.6), whereas doubling e (0.24 to 0.48 yr^{-1}) effectively drives P from 0.2 to zero.

Discussion

Comparison of model simulations with present observations

From this model analysis, we conclude that under prolonged (metapopulation time scales of decades) and intensive fishing ($e_F > e_N$), a northern cod metapopulation would decline as some subpopulations associated with major spawning locations are extirpated due to sustained over exploitation. The present model does not predict which subpopulations depicted in Fig. 1 would become extinct, only that the number of spawning areas occupied (P) would be reduced. If harvesting does not increase to the point where the persistence of the entire metapopulation is threatened ($e_F + e_N > m$), the system will reach a new equilibrium, albeit with fewer subpopulations than prior to exploitation.

This prediction of the model is supported by recent observations. Myers et al. (1997a) used mark-recapture data to estimate that since the 1940s, exploitation rates of inshore stock components of northern cod have been very high, with instantaneous fishing mortalities (F) exceeding unity (> 63% mortality per year) in the 1980s and early 1990s. Inshore subpopulations could be extirpated under such levels of fishing harvest. Our model hindcasts the decline in spawning area occupancy exhibited by northern cod during the past decade, where the fish were found overwintering/spawning at few offshore areas (Kulka et al. 1995, Hutchings 1996, Rice 1997). Currently, only 5 spawning areas are occupied by northern cod, including Trinity and adjacent Bonavista Bay in eastern Newfoundland (Smedbol et al. 1998), Gilbert Bay in southern Labrador (Ruzzante et al. 2000), the northern Grand Bank (e.g. Shelton et al. 1996), and the southern edge of Hamilton Bank (G. Rose, Fisheries Conservation Chair, Memorial University of Newfoundland, personal communication). $P = 0.5$ is similar to the current situation, when significant spawning occurs at only 5 of 11 areas identified in Fig. 1.

Model predictions of northern cod population recovery

Metapopulation modelling provides insight as to how the northern cod population might recover, in terms of the reoccupation of currently empty spawning areas within its historical geographic range. Since the summer of 1992 the northern cod stock complex has been under a commercial fishing moratorium. A limited fishery (9000 mt quota) conducted within 12 n. mi. of the eastern Newfoundland-Labrador coastline was resumed in 1999. If adult cod aggregations are the agents of recolonization of unoccupied spawning areas, then resumption of fishing will inhibit the recovery of the northern cod metapopulation. Fishing harvest might affect the recovery by removing excess individuals from occupied areas, thereby preventing these individuals from serving as colonizing immigrants to currently unoccupied areas, in effect lowering m. Table 1 shows two possible effects of fishing harvest upon metapopulation recovery by increasing $e_F > 0$: (i) the length of time required for recovery to a new equilibrium state (P_E) is greater than the time needed under a moratorium ($e_F = 0$), and (ii) the number of subpopulations existing at the new equilibrium

state (P_E) will be lower than the number existing in the absence of commercial harvesting ($e_F = 0$).

Supporting evidence for these model predictions can be obtained from documented changes in the northern cod fishery. Intense overfishing from 1965-1969 decimated the subpopulations associated with Saglek, Nain, and Makkovik-Harrison Banks off northern Labrador (Fig. 1) (NAFO Divisions 2G and 2H). These subpopulations have yet to recover, and commercial catches in these areas have remained low since the early 1970s (Lear & Parsons 1993). In fact, the lack of recovery in these areas is the reason cited for their exclusion from the management unit of the northern cod stock, designated as NAFO Divisions 2J3KL. The range of the northern cod stock is now considered to extend from Hamilton Bank to the northern part of the Grand Bank (Pinhorn 1976), even though Saglek, Nain and Makkovik-Harrison Banks were once northern components of the northern cod stock complex (Lear & Parsons 1993). This new state also demonstrates the discreteness (semi-isolation) of the local population dynamics of the constituent subpopulations, which is one of the defining characteristics of metapopulation structure.

During the seven years since the northern cod stock was placed under a commercial fishing moratorium (1992), and there has been no evidence of recovery in either abundance of the stock complex or recolonization of historical spawning areas to the north (DFO 1999). In contrast, the metapopulation model predicts a partial recovery (Table 1). Why is there no sign of the predicted recovery?

One reason may be that the remaining subpopulations have not increased in abundance to the point where sufficient numbers of colonizers have been produced. The population growth rates of local populations are relatively low. Myers et al. (1997b) estimated a maximum intrinsic rate of natural increase of $r_m = 0.17$ yr^{-1} for the northern cod stock. This value of r_m was one of the lowest rates in an analysis of 20 different Atlantic cod stocks. Moreover, abundance may have been reduced by losses due to unintended harvesting. Even during the moratorium, northern cod were taken as bycatch in fisheries for other species. Another possibility for the absence of a detectable recovery may be the loss of individuals through increased natural mortality. The impact of predation upon northern cod by the harp seal (*Phoca groenlandica*) is being investigated (Gagné 1999).

Localized collapses and recoveries during the history of the northern cod fishery tended to occur over 10-30 year periods (see Lear & Parsons 1993, Hutchings & Myers 1995). This time scale is similar to historical collapse and recovery periods reported for other Atlantic cod fisheries in Greenland (e.g. Cushing 1982), Iceland (Jónsson 1994), and the Barents Sea (Øiestad 1994).

Decreasing the model values of m and e each by an order of magnitude results in the same equilibrium value of P_E, but the time to recovery becomes unrealistically long (order 50 years).

The genetic evidence for metapopulation structure in northern cod (e.g. Ruzzante et al. 1997, Ruzzante et al. 2000) reflects past spatial dynamics. If differences in microsatellite DNA allele frequencies exist at the subpopulation level, then the number of reproductively successful individuals exchanged between subpopulations must be relatively low; otherwise such differentiation would not have developed. However present structure does not predict how recolonization of unoccupied areas will occur. Mark-recapture studies of migrating adult cod (e.g. Lear 1984) and the drift of eggs and larvae (e.g. Helbig et al. 1992) suggest recolonization events are possible.

Critique of the metapopulation model

In our metapopulation model, geographic area is treated implicitly rather than explicitly (realistically). Each subpopulation is considered to be equally connected (by exchanges) to each other, and thus their relative locations in space are ignored. The northern cod population is not a Levins (1970) style metapopulation wherein all subpopulations are equal in size. For example, the subpopulation associated with the area of Hamilton Bank is orders of magnitude larger than the Gilbert Bay subpopulation located in that small, 15 km long bay (Fig. 1). The actual number of spawning areas occupied historically by northern cod is not known, and could be greater than the 11 areas identified in Fig. 1. Additional subpopulations may have existed, likely relatively small in area and abundance, in the fjords and bays of central and northern Labrador.

The next step in the development of metapopulation theory for the northern population would be to construct a spatially realistic model. A spatially realistic metapopulation model incorporates all information concerning the number, size, exact location, and connectivity of habitat patches (Hanski 1994b, Hanski & Simberloff 1997). Such models allow quantitative predictions about the dynamics of metapopulations (Hanski & Simberloff 1997). A spatially realistic metapopulation model would include specific exchange rates between all possible pairs of subpopulations within the metapopulation.

In our metapopulation model for northern cod, local population dynamics such as growth and predation are ignored. The model estimates the proportion of suitable areas that are occupied, not the number of individuals in each area. A more realistic model would include treatment of the demographics of subpopulations, with implications for recolonization. Presently, data on the population dynamics for all putative subpopulations does not exist. Rather, abundance estimates exist only at the scale of the entire metapopulation (northern cod stock complex), and only for a relatively short time series (approximately 20 years, DFO 1999).

Metapopulation structure in other marine fishes

We hypothesize that other cod populations with large geographic ranges exhibit metapopulation structure during a segment of their reproductive cycle. During the pre-spawning and spawning seasons many cod populations exhibit high intra-annual variance in

regional density. Individuals from local populations often display strong interannual fidelity to specific geographical spawning areas (Harden-Jones 1968).

This spatial segregation during the spawning season occurs in cod (*Gadus morhua*) stocks off Norway, where coastal (fjord) cod are considered to be genetically and behaviourally distinct from migratory Northeast Arctic cod (Jakobsen 1987, Dahle 1991, Salvanes & Ulltang 1992, Dahle & Jørstad 1993). Northeast Arctic cod spawn in several areas along the nearshore banks. Spawning occurs mainly at Lofoten, but also to the North near Sørøy and to the south as far as Møre (Bergstad et al. 1987). Evidence from tagging experiments indicates that spawners return to their location of first spawning in subsequent spawning seasons (Gødø 1984). Coastal cod, found in the fjords and nearshore areas of Norway, are considered a subpopulation separate from Northeast Arctic cod (Gødø & Moksness 1987). The spawning subpopulations in the coastal areas are often comprised of two elements. One unit is resident in the area year-round, and the other unit includes individuals that migrate from neighbouring fjords and offshore areas (Gødø 1984, Jakobsen 1987, Salvanes & Ulltang 1992), yet these subpopulations remain genetically distinct. Regardless of the degree of genetic distinctness, it is important to note that both inshore (Jakobsen 1987) and offshore (Bergstad et al. 1987) spawning occurs in predictable areas year after year.

In addition to the Alaskan pollock (Bailey 1998, Bailey et al. 1999), other semi-pelagic fish populations may be structured as metapopulations. The Barents Sea saithe (*Polliachius virens*) is another abundant, commercially exploited population that occupies discrete spawning areas within its overall range. Saithe spawn on the coastal banks off Møre, Haltenbanken and Lofoten, and in the northern North Sea (Bergstad et al. 1987). This stock has shown fairly substantial emigration to stocks found around Iceland and the Faroe Islands (Jakobsen & Olsen 1987).

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Table 1. Years required to reach the equilibrium number of subpopulations under a range of initial occupancies. The colonization parameter is held constant at $m = 0.3$ yr^{-1}, and the extinction parameter is increased to simulate the effect of fishing ($e = e_N + e_F$, where $e_N = 0.03$ yr^{-1}). The equilibrium proportion of occupied areas (P_E) is listed below the e_F value.

	Length of time required to reach equilibrium proportion of occupied areas (years)				
Initial proportion of occupied areas (P)	$e = 0.03$ ($P_E = 0.9$)	$e = 0.06$ ($P_E = 0.8$)	$e = 0.09$ ($P_E = 0.7$)	$e = 0.12$ ($P_E = 0.6$)	$e = 0.15$ ($P_E = 0.5$)
0.1	27	29.5	32.5	35.5	40
0.2	24	26	28	30.5	33.5
0.3	22	23.5	25	27	28
0.4	20.5	21.5	22.5	23	21.5
0.5	18.5	19	19.5	18	0
0.6	17	17	15	0	19
0.7	15	13.5	0	15.5	22.5
0.8	12	0	14	19	24.5
0.9	0	12.5	16.5	21	25.5
0.95	8.5	13.5	17.5	21.5	26

Figure captions

Fig. 1. Bathymetric chart of the northwest Atlantic shelf, showing the major banks and the Northwest Atlantic Fishery Organization (NAFO) management units (2GHJ, 3KL) off Newfoundland and Labrador. Shaded regions are known spawning areas and locations of proposed subpopulations of a northern cod metapopulation. Subpopulations joined by heavy lines denote a "mixed structure" that may function as a single subpopulation. Question marks denote possible subpopulations.

Fig. 2. Metapopulation structures, redrawn from Harrison and Taylor (1997). Shaded regions are subpopulations; unfilled regions are unoccupied subpopulation areas; dotted lines are boundaries of subpopulations; arrows indicate exchange between subpopulations. (a) A simple Levins (1970) metapopulation. (b) A mixed structure metapopulation where subpopulations with high rates of exchange are combined into a singe subpopulation. Local populations with greater isolation may become extinct and later recolonized.

Fig. 3. Conceptual diagram relating subpopulation structure to northern cod life history. Dotted lines are boundaries of subpopulations; thin arrows encircling spawning areas represent ocean currents and eddies which promote retention of drifting eggs and larvae.

Fig. 4. Three-dimensional representation of the equilibrium solution (Eq. 2 in text) for the Levins (1970) metapopulation model, showing the change in proportion of occupied spawning areas (P) under a range of colonization (m) and extinction (e) parameter values.

Fig. 5. Fig. 4 redrawn to show values of P along (a) isopleths of e and (b) isopleths of m.

Fig. 6. Time dependent solution of the Levins model, under a range of initial values for P and values of m and e estimated for the northern cod metapopulation. (a) Base case for an unfished northern cod metapopulation: $m = 0.3\ yr^{-1}$, $e = 0.03\ yr^{-1}$. (b) Solution where m is half its estimated value: $m = 0.15\ yr^{-1}$, $e = 0.03\ yr^{-1}$. (c) Solution where e is twice its estimated value: $m = 0.3\ yr^{-1}$, $e = 0.06\ yr^{-1}$. (d) Solution for an overexploited northern cod metapopulation: $m = 0.3\ yr^{-1}$, $e = 0.24\ yr^{-1}$.

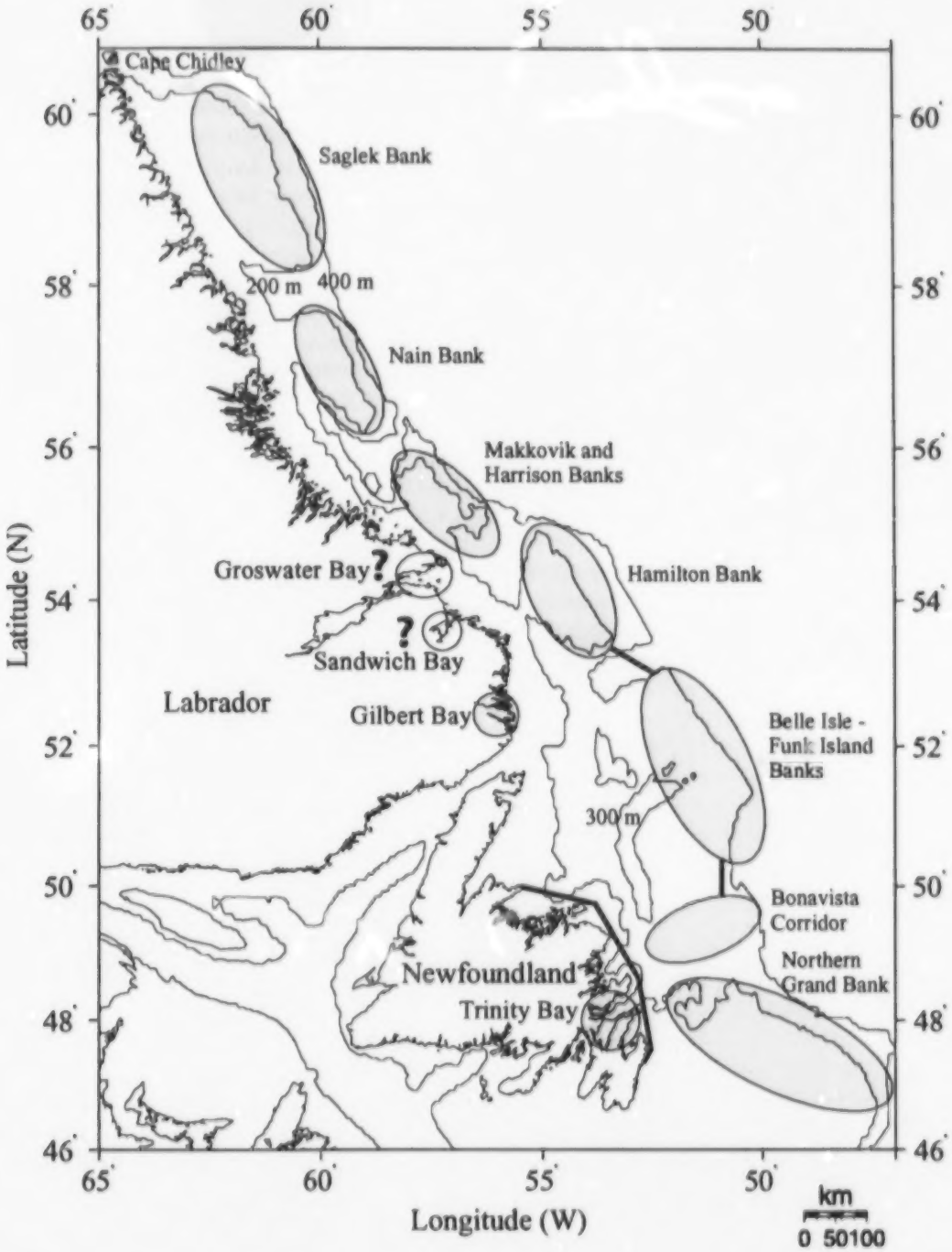
65
60
55
50
Cape Chidley
60
Saglek Bank
58
200 m
400 m
Nain Bank
56
Makkovik and
Harrison Banks
Groswater Bay?
Hamilton Bank
54
?
Sandwich Bay
Labrador
Gilbert Bay
52
Belle Isle -
Funk Island
Banks
300 m
50
Bonavista
Corridor
Newfoundland
Northern
Grand Bank
Trinity Bay
48
46
Latitude (N)
Longitude (W)
km
0 50100

Fig. 1

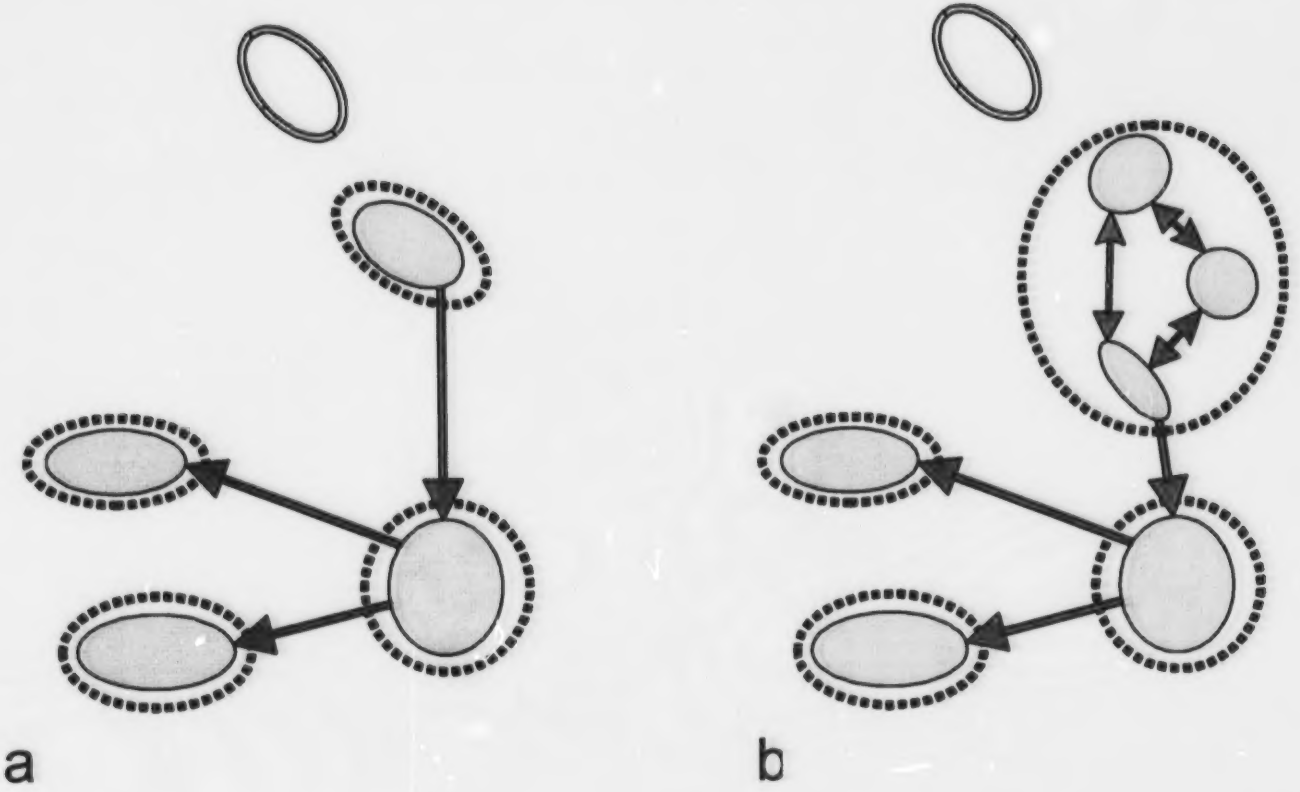

Fig. 2

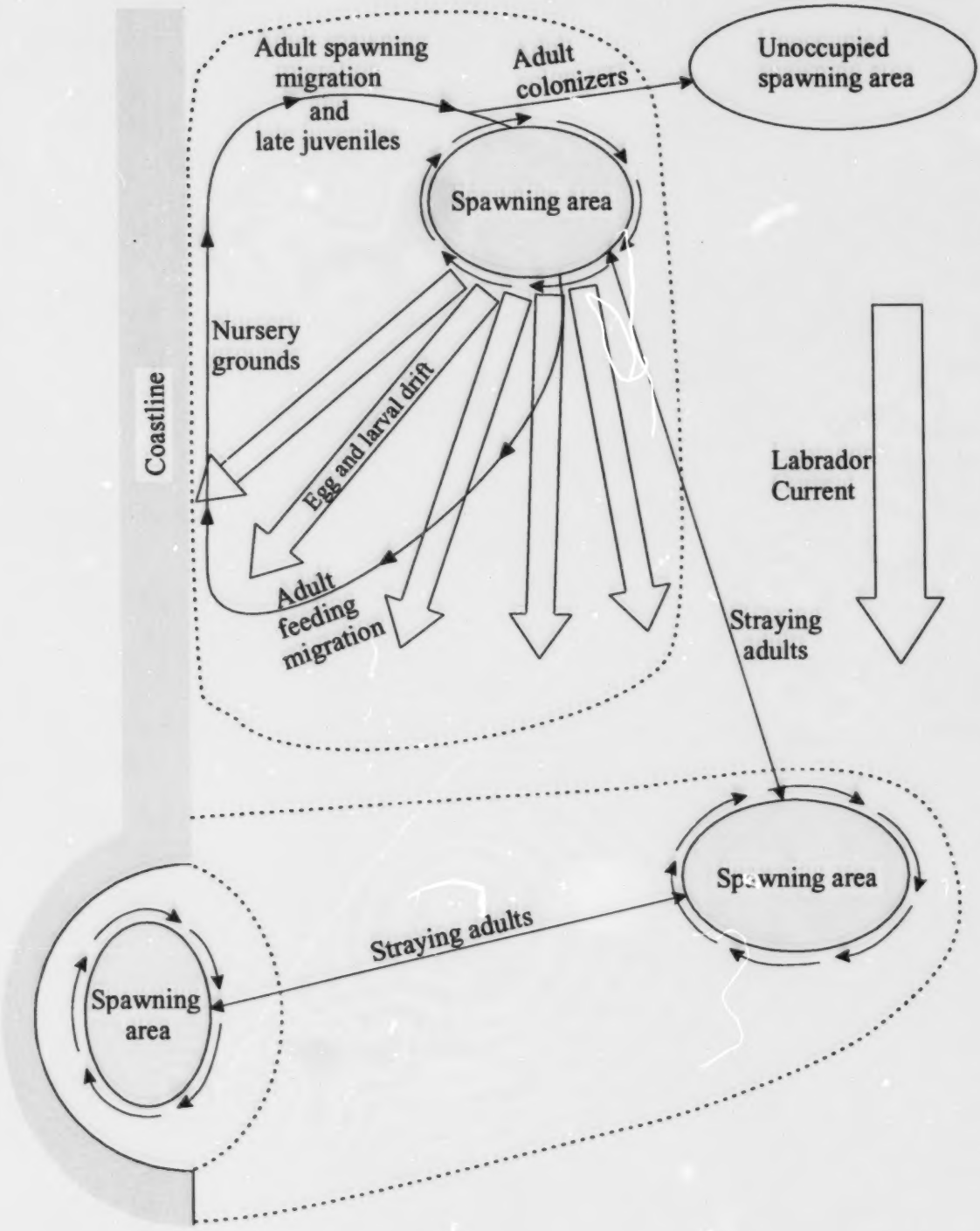
Adult spawning migration and late juveniles
Adult colonizers
Unoccupied spawning area
Spawning area
Nursery grounds
Egg and larval drift
Coastline
Labrador Current
Adult feeding migration
Straying adults
Spawning area
Straying adults
Spawning area

Fig. 3

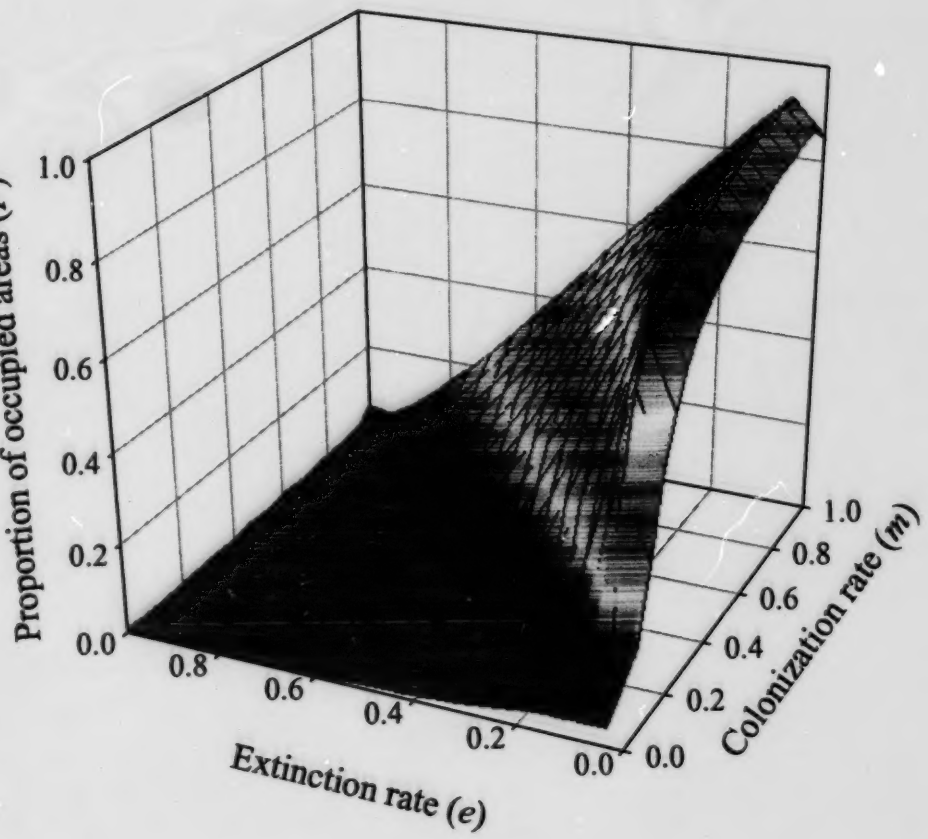
Proportion of occupied areas (P)
1.0
0.8
0.6
0.4
0.2
0.0
0.8
0.6
0.4
0.2
0.0
Extinction rate (e)
0.0
0.2
0.4
0.6
0.8
1.0
Colonization rate (m)

Fig. 4

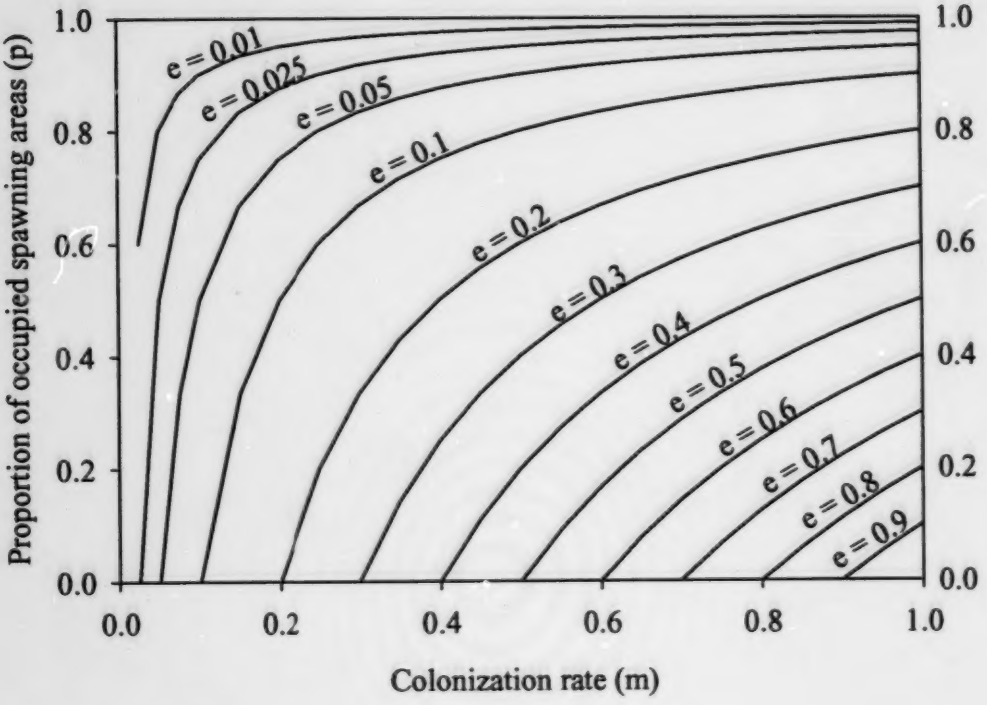
Proportion of occupied spawning areas (p)
Colonization rate (m)
e = 0.01
e = 0.025
e = 0.05
e = 0.1
e = 0.2
e = 0.3
e = 0.4
e = 0.5
e = 0.6
e = 0.7
e = 0.8
e = 0.9
0.0
0.2
0.4
0.6
0.8
1.0

Fig. 5

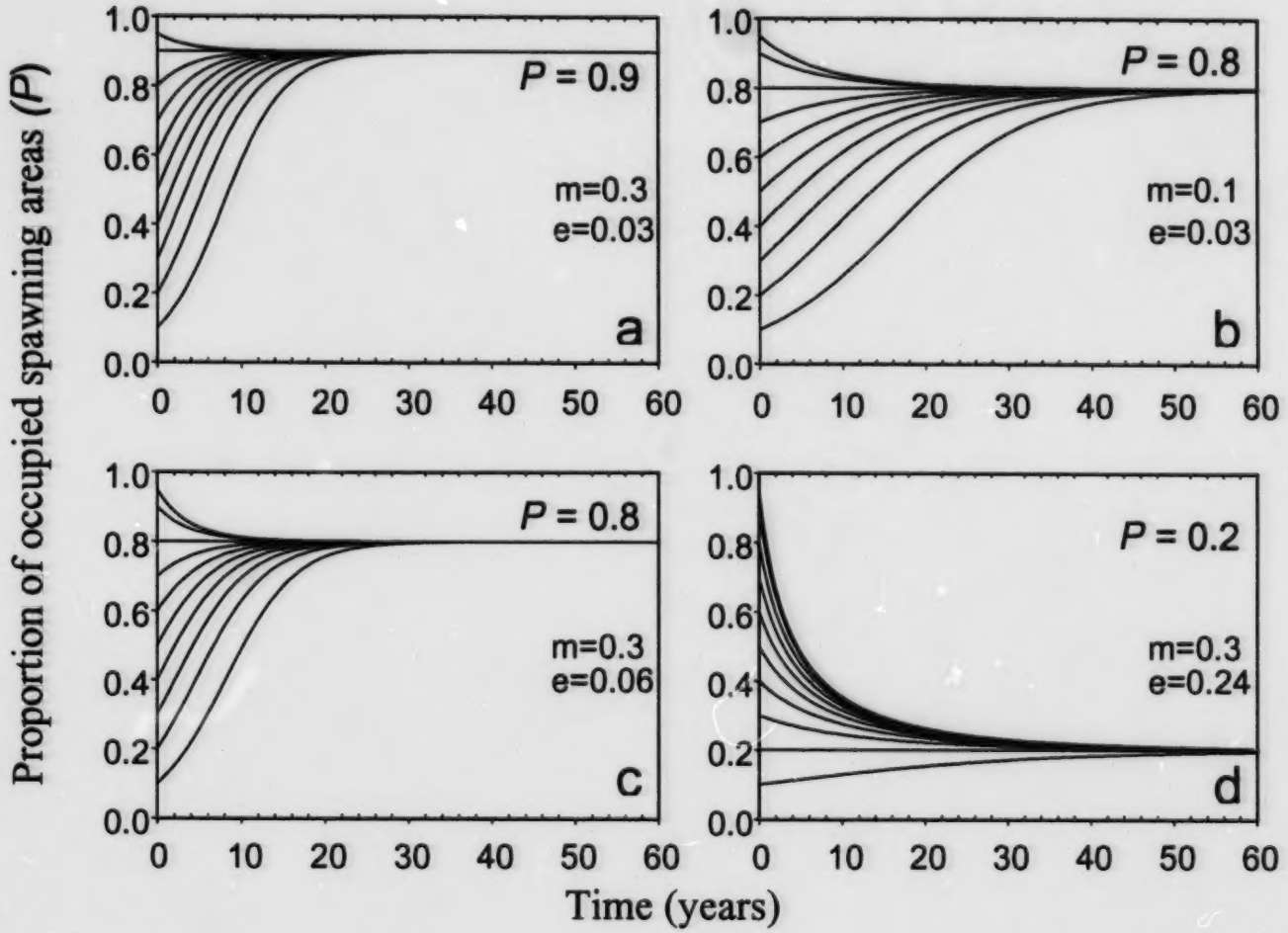
Proportion of occupied spawning areas (P)
P = 0.9
m=0.3
e=0.03
a
P = 0.8
m=0.1
e=0.03
b
P = 0.8
m=0.3
e=0.06
c
P = 0.2
m=0.3
e=0.24
d
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
60
Time (years)

Fig. 6